HISTOLOGY AND MORPHOLOGY OF THE SCALES IN SOME EXTINCT AND EXTANT TELEOSTS

by

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ABSTRACT. - Scale morphology and histology of some fossil and extant teleosts, as well as some stem group teleosts such as Pachycormiforms, are compared. Basal teleosts have lepidosteoid type scales, although cycloid scales appear at the †*Leptolepis coryphaenoides* level. Pachycormiforms have mainly lepidosteoid scales, but amioid type scales also occur within this clade, confirming that pachycormiforms are not teleosts. An osteoglossid type of scale is defined, based on morphological and histological characters and is considered a derived feature within teleosts.

RÉSUMÉ. - Histologie et morphologie de quelques écailles des téléostéens basaux actuels et fossiles.

La morphologie et l'histologie des écailles de quelques téléostéens fossiles et actuels sont comparées à celles de quelques groupes souches de téléostéens tels que les Pachycormiformes. Les téléostéens basaux ont des écailles de type lépidostéoïde, alors que le type élasmoïde n'apparaît qu'avec †*Leptolepis coryphaenoides*. Les Pachycormiformes ont principalement des écailles lepidostéoïdes, mais des écailles de type amioïde sont également connues dans ce clade ; ceci confirme que les pachycormiformes ne sont pas des téléostéens. Un type d'écaille ostéoglossoïde est défini sur la base de caractères morphologiques et histologiques ; ces écailles sont considérées comme dérivées parmi les téléostéens.

Key words. - Pachycormiformes - Basal teleosteans - Amioid scales - Lepidosteoid scales - Elasmoid scales - Osteoglossoid scales - Paleohistology.

Teleostei comprises the most species-rich assemblage within vertebrates (Nelson, 1994), with an estimated 28,500 valid extant species (Froese and Pauly, 2004). However, the monophyletic condition of the Teleostei, especially with respect to Mesozoic basal teleosts *sensu* Patterson (1973, 1977) and Patterson and Rosen (1977), is an ongoing debate. Some groups previously considered as basal teleosts by Patterson (1973, 1977) have been re-studied, and new phylogenetic hypotheses of relationships have been proposed. Some taxa, such as the †pachycormids, are considered as non-teleosts (Brito, 1997; Arratia 1999, 2000a, 2000b contra Pinna, 1996), while others such as the †aspidorhynchids remain controversial (e.g. either basal teleosts for Pinna, 1996; Brito, 1997, 1999; Brito and Meunier, 2000, or stem-group teleosts, or simply non teleosts according to Arratia, 1999, 2000a, 2000b). The †pleuropholids and †ichthyokentemids are now considered stem-teleosts (Arratia, 2000a), and the †pholidophorids are considered to be a paraphyletic assemblage comprising some non-teleost taxa (Arratia and Tintori, in prep.). The Teleostei are consensually accepted above the level of †*Pholidophorus bechei*.

Considerable debate is still remaining with regard to the position of the elopomorphs and osteoglossomorphs within the Teleostei (Patterson and Rosen, 1977; Arratia, 1997, 1998; Patterson, 1998), with the Elopomorpha possibly being a paraphyletic group (Filleul and Lavoué, 2001). Although this debate will continue, we propose here to examine the histology and morphology of the scales of some neopterygians considered as basal teleosts. We focus mainly on the patterns of transitions in these groups in an attempt to contribute to a better understanding of the relationships within this group, and to show that the scales of the Actinopterygii, and especially those of the Teleostei, may provide valid phylogenetic information (Khemiri *et al*., 2001). We also offer interpretations on some aspects of the transformation of ganoid scales into elasmoid scales, and we try to identify homologous structures between ganoid and elasmoid scales in the teleostean lineage.

MATERIAL AND METHODS

This study is based on extinct and extant taxa considered as basal teleosts. Given the taxonomic problems found in some Mesozoic families that seem to be polyphyletic (e.g., †Pholidophoridae, †Leptolepidae), the choice of taxa was crucial for our analysis. For this reason, we chose the most complete specimens in an attempt to obtain the broadest view possible.

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Cybium 2004, 28(3): 225-235.

Histo-morphological descriptions are followed by specific comments where deemed necessary. The external surface of ganoin was observed using a scanning electron microscope (SEM). Ground cross sections were made as described by Matrajt *et al.* (1967), modified by Meunier *et al.* (1978).

This work is based on specimens belonging to the collections in the Muséum national d'Histoire naturelle, Paris (MNHN). All the scales were sampled on well-determined, articulated or semi-articulated specimens. The following taxa were examined:

Fossil material

†*Pachycormus macropterus*. - MNHN-ICH 289, Upper Lias, La Caine, France. †*Aspidorhynchus acutirostris*. - MNHN-ICH 260, Tithonian of Solnhofen, Germany and Upper Kimmeridgian of Cerin, France. †*Aspidorhynchus euodus*. - MNHN-ICH 263, Callovian of Cambridgeshire, UK. †*Belonostomus tenuirostris*. - MNHN-ICH 264, Tithonian of Solnhofen, Germany and Upper Kimmeridgian of Cerin, France. †*Vinctifer comptoni*. - MNHN-ICH 259, MNHN-ICH 261, Albian, Santana Formation, Brazil. †*Pholidophorus bechei*. - MNHN-ICH 285, Lower Lias, Dorsetshire, UK. †*Pholidophorus latiusculus*. - MNHN-ICH 290, Late Triassic, Italy. †*Pholidophorus*? sp. - MNHN-ICH 265, Late Jurassic of Normandy, France. †*Siemensichthys macrocephalus*. - MNHN-ICH 286, Tithonian of Solnhofen, Germany. †*Ichthyokentema purbeckensis*. - MNHN-ICH 244, Lower Purbeckian, Isle of Portland, UK. †*Gondwanapleuropholis longimaxillaris*. - MNHN-ICH 291, ?Late Jurassic, Pastos Bons Formation, Brazil. †*Laelichthys ancestralis*. - MNHN-ICH 284, Aptian, Areado Formation, Brazil.

Extant material

The study of fossil material was complemented by observation of scales in extant basal teleosts. Part of this material has been studied in previous papers (e.g., *Arapaima gigas* and *Osteoglossum biccirhosum* in Meunier, 1984a; *Hoplias aimara* in Meunier, 1997). Other, uncatalogued material, will be described in a separate note.

Osteoglossomorpha: *Arapaima gigas, Osteoglossum biccirhosum, Marcusenius ussheri, Notopterus notopterus, Hiodon alosoides*;

Elopomorpha: *Megalops atlanticus, Albula vulpes*;

Clupeomorpha: *Clupea harengus*;

Ostaryophysi: *Chanos chanos, Hoplias aimara, Cyprinus carpio*.

RESULTS

The scales can be divided into two main types: ganoid and elasmoid.

Ganoid scales

The scales of †*Aspidorhynchus acutirostris*, †*Belonostomus tenuirostris*, †*Vinctifer comptoni*, †*Pholidophorus bechei*, †*P. latiusculus*, †*Pholidophorus*? sp. from Normandy, †*Siemensichthys macrocephalus*, †*Ichthyokentema purbeckensis*, †*Gondwanapleuropholis longimaxillaris* have a rhombic shape. They are thick, juxtaposed, and display a peg-and-socket articulation.

The general structure of the scales in all of the "ganoid" taxa is basically similar (Figs 1-6). They all show the lepidosteoid features, presenting a bony basal plate with osteocyte spaces (osteocytic bone of Weiss and Watabe, 1979) (Figs 1, 3), overlain by a layer of ganoin of variable thickness, generally composed of several sheets (Figs 1, 3, 5, 6), and lacking an intercalated dentin layer (Goodrich, 1907; Schultze, 1966, 1977, 1996; Ørvig, 1977; Sire and Meunier, 1994; Brito *et al.*, 2000). The external surface of the ganoin layer shows the characteristic tubercles in †aspidorhynchids (see Brito and Meunier, 2000), as found in some †palaeoniscoid scales (Schultze, 1966; Ermin *et al.*, 1971; Gayet and Meunier, 1986; Richter and Smith, 1995). The unique exception is found in †*Pholidophorus*? sp., from the Late Jurassic of Normandy (France), where the scale surface is uneven and lacks tubercles (see below).

The scales of †*Aspidorhynchus acutirostris* have no ganoin preserved (Schultze, 1966, 1996; Brito and Meunier, 2000), while in †*Aspidorhynchus euodus* a thin ganoin layer (Fig. 7) is present (Brito and Meunier, 2000).

†*Pholidophorus*? sp. from the Late Jurassic of Normandy (France) possesses scales of the lepidosteoid type, although the external surface does not show the minute tubercles, characterizing ganoin. The ganoin is pluri-stratified, and overlain by a mineralized, irregular layer (Figs 3, 4). This external layer shows thin, irregular lines of incremental growth and contacts the bony basal plate at the margin scale (see Figs 3, 4).

In species with ganoid scales, the bony plate has Sharpey's fibers, which are interconnected with neighbouring scales and the dermis (Fig. 2). The basal plate also shows a central area of woven bone (*sensu* Francillon-Vieillot *et al.*, 1990) (Fig. 8), with thin layers of lamellar bone above, and a thicker layer of lamellar bone below (Fig. 9). The lamellae are between 0.5 and 2 μm in thickness, and they are alternatively bright or dark under polarized light (Figs 8, 9). The woven bone shows isodiametric osteocytes (Fig. 3), whereas the osteocytes of lamellar bone are flat and located between the bone strata (Figs 1, 2).

In all the species examined the basal plate is crossed by numerous canals of Williamson, 1.5 to 4 μm in diameter (Figs 1, 3, 6). The scales lack vascular canals.

Elasmoid scales

In †*Pachycormus macropterus*, †*Leptolepis coryphaenoides*, †*Laelichthys ancestralis*, *Arapaima gigas*, *Osteoglossum biccirhosum*, *Marcusenius ussheri*, *Notopterus notopterus*, *Hiodon alosoides*, *Megalops atlanticus*, *Albula vulpes, Clupea harengus, Chanos chanos, Hoplias aimara,* and *Cyprinus carpio* scales are thin and imbricated.

Three main types of elasmoid scales are generally encountered in actinopterygian fishes: amioid scales, with radial ridges on the overlapped field (Schultze, 1977, 1996); cycloid scales with a smooth posterior margin (Figs 13, 16), and ctenoid scales with a posterior margin ornamented with acute denticles, the ctenii; cycloid and ctenoid scales have concentric circuli on the anterior overlapped field (Bertin, 1958). However, no ctenoid scales, which are found essentially in derived teleosts (Roberts, 1993), were present in the samples studied.

†*Pachycormus macropterus* is the only taxon that possesses scales of the amioid-type (not illustrated). These scales consist only in a relatively thin stratified bony basal plate surmounted by radial structures. Despite the fact that these structures are apparently comparable to those in amiids and other halecomorphs, in †*Pachycormus macropterus* the ridges seem to be much thinner.

†*Laelichthys ancestralis*, generally considered to be closely related to the Osteoglossidae, has thin imbricated scales showing radiating grooves, but squamulae are absent. The structure is similar to that of elasmoid scales in extant taxa (but see below) with a basal plate showing several layers 4 μm thick in average, forming a double-twisted 'plywood' texture (Fig. 10). Osteocyte lacunae are seen in the superficial layer.

The cycloid scales of extant teleosts show various types of ornamentation on their outer surface. Often, a variable number of concentric, circular ridges (circuli) and radial grooves (radii), radiating from the center (focus) of the scale are present (Figs 13, 16). Moreover, in some fishes, the relief is obscured by various superficial structures, such as sharp or smooth, tooth-like ornamentation. Whatever the origin of this ornamentation, two main kinds of cycloid scales occur. The first type is found in the scales of *Arapaima gigas*, *Osteoglossum biccirhosum* and *Marcusenius ussheri,* in which the surface lacks radii, but presents grooves that divide the entire surface into a mosaic of polygonal plates, termed squamulae (Fig. 14). The squamulae are ornamented either with acute protuberances (Osteoglossidae) or with circuli (Mormyridae) (see Meunier, 1984a). In the posterior field of the scales, these protuberances fuse, forming irregular tubercles, as in *Arapaima gigas*. The second kind of cycloid scale is typical of most teleosts, and is found in *Notopterus notopterus, Hiodon alosoides, Megalops atlanticus, Albula vulpes, Clupea harengus, Chanos chanos* and *Cyprinus carpio*. In these scales, a large number of circuli (surmonted by small denticles), can be distinguished. The density of these circuli varies according to the species examined. Some scales in *N. notopterus, H. alosoides*, and *C. harengus* have the same ornamentation in the anterior and posterior fields. In these scales, smooth, regular and spaced circuli occur. *H. alosoides* has straight radii distributed over the entire scale surface, but in *N. notopterus*, the radii are limited to the anterior field. In *C. harengus,* the radii are transverse and are found over the entire surface of the scale. All other elasmoid scales examined do not show the same superficial ornamentation in the anterior and posterior fields. In *A. vulpes* and *C. chanos*, the circuli in the posterior field are replaced anteriorly by tubercles. In *A. vulpes* these tubercles are round while they are acute in *C. chanos* and limited to the central part of the scale. Some radii divide the anterior field of the scales of *A. vulpes*, although there are usually a smaller number of radii in *C. chanos*. *M. atlanticus* has pointed tubercles partly fused to each other in the posterior field of the scale, circuli surmounted by denticles in the posterior field, and two or three radii dividing both fields. The outer layer, termed "outer limiting layer" (Schönbörner *et al*., 1979), can thicken during ontogeny by the addition of thin incremental lines over the preceding ones (Fig. 12), especially in the posterior area.

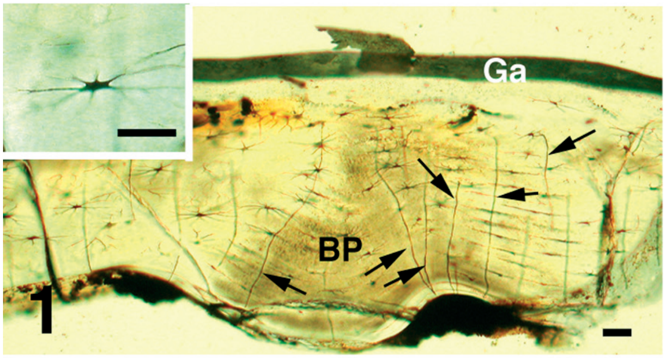
Among all the cycloid scales, only those belonging to *Arapaima gigas, Osteoglossum biccirhosum*, and *Megalops atlanticus* have embedded isodiametric star-shaped cells, or osteocytes, in their external layer. This layer, relatively slender in the anterior field of the scale, can thicken posteriorly in *A. gigas* and *M. atlanticus*.

In *A. gigas*, *H. alosoides, M. atlanticus* and *C. chanos*, cells are also embedded in the organic matrix of the basal plate; these cells, called elasmocytes (Meunier, 1984b; Francillon-Vieillot *et al*., 1990), are situated between the layers with their cytoplasmic processes extending along the collagen fibers. The elasmocytes are distributed evenly in the scale, but they are only located in the first two layers of the basal plate, except in *A. gigas* in which they are present throughout the basal plate. No cell is observed in the basal plate of *Notopterus notopterus* and *Clupea harengus*.

The basal plate consists of layers of collagen fibrils superimposed in various directions from one layer to the other. Ground sections under polarized light show a series of layers of variable brightness. This indicates that the orientation of the collagen fibrils is different in the successive layers. This spatial organization of collagen fibrils characterizes a twisted plywood-like structure (Meunier and Castanet, 1982).

Scale mineralization

Ganoid scales examined consist in mineralized tissues: ganoin (which is hypermineralized) and bony basal plate. The later is entirely mineralized, in contrast to that of the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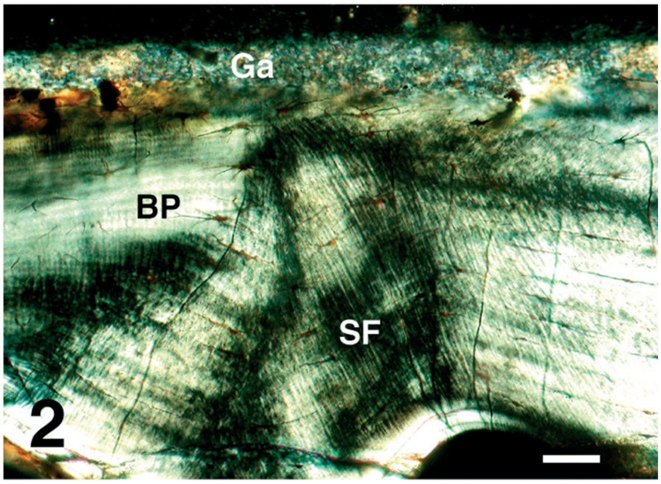
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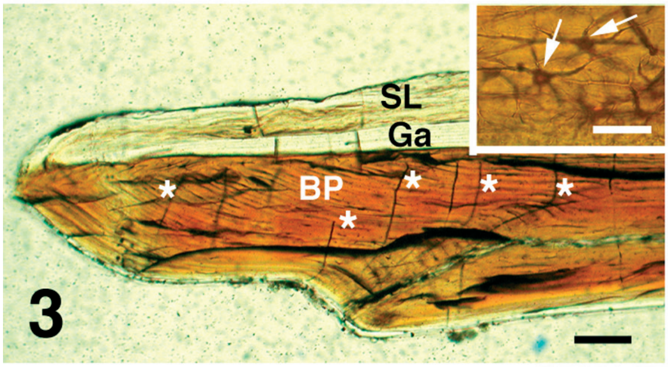
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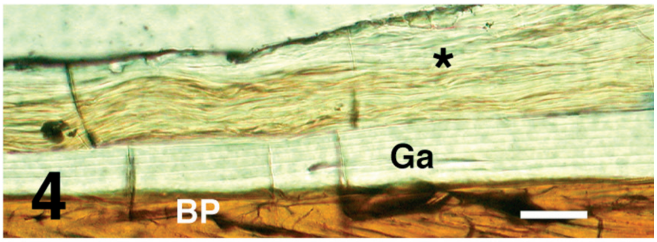
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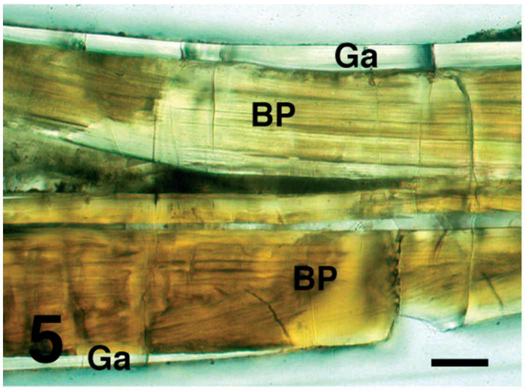
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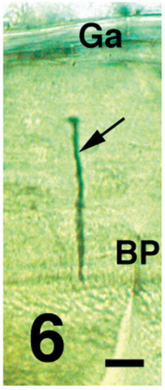
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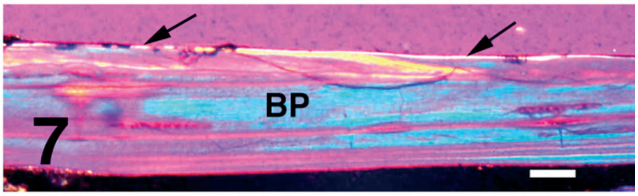
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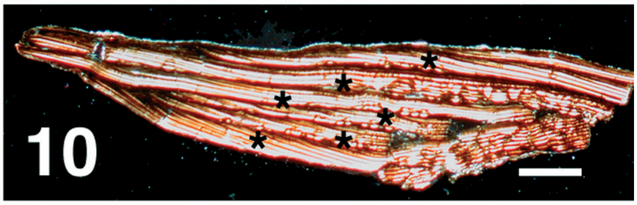
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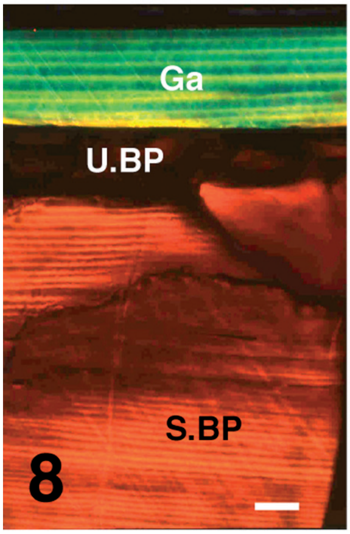
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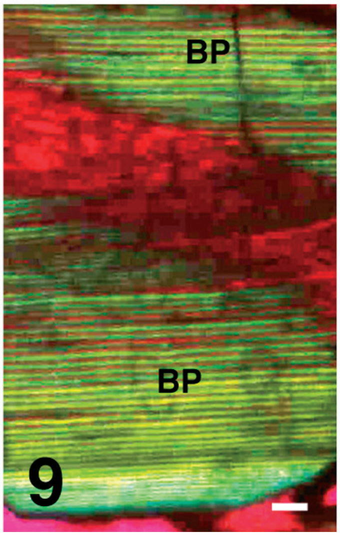
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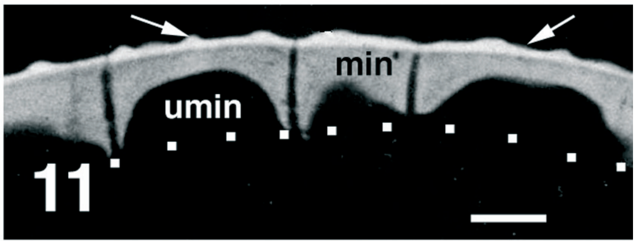
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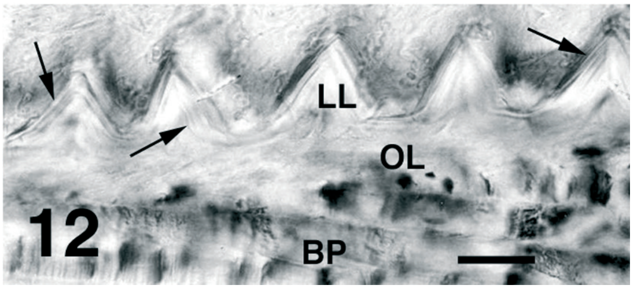
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elasmoid scales, which shows a different mode of mineralization, depending on the species (Meunier, 1984b). In extant taxa, the mineralizing front progresses by production and fusion of corpuscles of Mandl (Schönbörner *et al*., 1981; Zylberberg *et al*., 1992). However, such corpuscles lack in *Arapaima gigas* (see figs 20-22 in Meunier, 1984a).

In the scales of *Osteoglossum biccirhosum* and *Marcusenius ussheri*, the mineralization occurs more rapidly at the margins of the squamules than in the center, resulting in a "box-like" shape after removal of the unmineralized organic matrix (Figs 11, 15). Such "box-like" shape is easily recognizable in fossil squamulae (Gayet and Meunier, 1983; Meunier, 1984a) because the unmineralized matrix has usually been removed during fossilization.

In other cycloid scales, Mandl's corpuscles have different shapes; they are generally ovoid or polygonal, and sometimes, depending on their position, they have various shapes within a same scale (Figs 17-19). They may also fuse and form more complex shapes. The deep surface of the scales of †*Laelichthys ancestralis* looks uneven in the SEM and high magnification indicates the presence of numerous, polygonal Mandl's corpuscles (Fig. 20).

In all scales studied, except in †*Pachycormus*, the basal plate is uncompletely mineralized, the mineralizing front being generally far from the scale surface where the collagen fibers are deposed.

Three types of mineralization can be recognized from the samples studied: the most frequent involves Mandl's corpuscles, as in †*Laelichthys ancestralis*, and in the recent teleost scales, except in Osteoglossidae and Mormyridae. These corpuscles are patches of mineral nucleation that form at a distance from the mineralizing front. Typically, they show polygonal shapes and as they grow, they progressively merge each with the other and, finally, merge with the mineralization front (Figs 18, 19). The second type of mineralization, the so-called "box-like" type, is found in Mormyridae (Fig. 15) and Osteoglossidae (excepting *Arapaima gigas*). In the basal plate the mineralization progresses faster near the margin than in the center of the squamulae (Fig. 11). It also progresses faster around the vascular canals, which cross the collagen layers. The third type of mineralization, as seen in *Arapaima gigas*, is a fairly regular progression of the mineralizing front. There is no mineral deposition immediately below the grooves, but mineralization is more important close to the vascular canals.

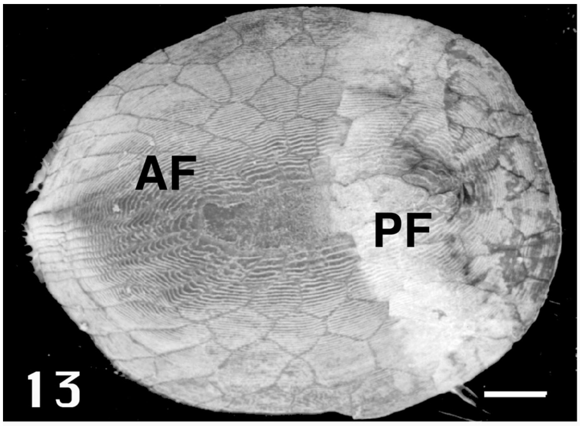
DISCUSSION

Scale structure in basal teleosts

The scales of †*Pholidophorus bechei*, †*P. latiusculus*, †*Pholidophorus*? sp., †*Siemensichthys macrocephalus*, †*Aspidorhynchus acutirostris*, †*Belonostomus tenuirostris*, †*Vinctifer comptoni*, †*Ichthyokentema purbeckensis*, and †*Gondwanapleuropholis longimaxillaris* are ganoid scales of the lepidosteoid type. The bony basal plate is directly overlain by ganoin, without an intercalated dentin layer (Goodrich, 1907; Schultze, 1977, 1996; Sire and Meunier, 1994). However, some variability exists within the †aspidorhynchids, in which, for instance, †*Aspidorhynchus* lacks ganoin (see discussion in Brito and Meunier, 2000).

In these extinct taxa and in the extant gars and polyp-

Figure 1. - †*Siemensichthys macrocephalus*. Ground section (MNHN-ICH 286). General view of a scale showing the ganoin layer (Ga) and the basal plate (BP) with osteocytes and transversecanals of Williamson (arrows); dentin is missing. Scale bar = 50 μm. Insert shows an enlarged osteocyte. Scale bar = 15 μm. • Figure 2. - †*Siemensichthys macrocephalus*. Detail of the section shown in figure 1 (polarized light) (MNHN-ICH 286). The basal plate (BP) is crossed by Sharpey's fibers (SF). Ga : ganoine. Scale bar = 50 μm. • Figure 3. - †"*Pholidophorus*"? sp. Ground section (MNHN-ICH 265). General view of a scale showing the ganoin layer (Ga) overlain by a superficial mineralized layer (SL) and the basal plate (BP) with transverse canals of Williamson (asterisks). There is no dentin layer. Scale bar = 100 μm. Insert shows two osteocytes (arrows) in the basal plate. Scale bar = 15 μm. • Figure 4. - †"*Pholidophorus*"? sp. Detail of the same section (MNHN-ICH 265). The ganoin layer (Ga) is clearly stratified and overlain by a superficial layer (asterisk) showing thin incrementing lines. BP : basal plate. Scale bar = 50 μm. • Figure 5. - †*Gondwanapleuropholis longimaxillaris*. Ground section (MNHN-ICH 291). General view of two opposite scales showing the ganoin layer (Ga) and the basal plate (BP). Scale bar = 50 μm. • Figure 6. - †*Gondwanapleuropholis longimaxillaris*. Ground section (MNHN-ICH 291). Detail showing the ganoin layer (Ga) and a canal of Williamson (arrow) in the basal plate (BP). Scale bar = 75 μm. • Figure 7. - †*Aspidorhynchus euodus*. Ground section (polarized light) (MNHN-ICH 263). Detail showing a very thin ganoin layer (arrows) made of one stratum, overlaying the basal plate (BP). Scale bar = 75 μm. • Figure 8. - †*Pholidophorus bechei*. Ground section (polarized light) (MNHN-ICH 285). Detail showing the ganoin layer (Ga) overlaying the basal plate that is constituted of an unstratified layer of woven bone (U.BP) and of a thick, stratified layer of lamellar bone (S.BP). Scale bar = 25 μm. • Figure 9. - †*Pholidophorus bechei*. Ground section (polarized light) (MNHN-ICH 285). Detail showing the basal plate (BP) with its regular plywood-like organization: alternatively light and dark layers. Scale bar = 25 μm. • Figure 10. - †*Laelichthys ancestralis*. Ground section (polarized light) (MNHN-ICH 284). Overview of six superposed scales (asterisks), showing the stratified basal plates (BP). Scale bar = 500 μm. • Figure 11. - *Osteoglossum biccirhosum*. Ground section (microradiograph). Detail showing the heterogeneous mineralization of the scale. The external layer is slightly more mineralized (arrows) than the basal plate, the calcification of which (min) grows faster below the superficial grooves than below the centre of the squamulae. Moreover, the basal plate does not mineralize in its entire thickness (umin). The dotted line indicates the deepest face of the scale. Scale bar = 250 μm. • Figure 12. - *Hoplias aimara*. Ground section. Detail showing the upper layers of the scale. The external layer is constituted of a bony layer (OL) that is overlain by the external limiting layer (LL). The latter clearly shows thin incrementing lines (arrows). The collagen layers of the basal plate (BP) underline the outer layer. Scale bar = 25 μm.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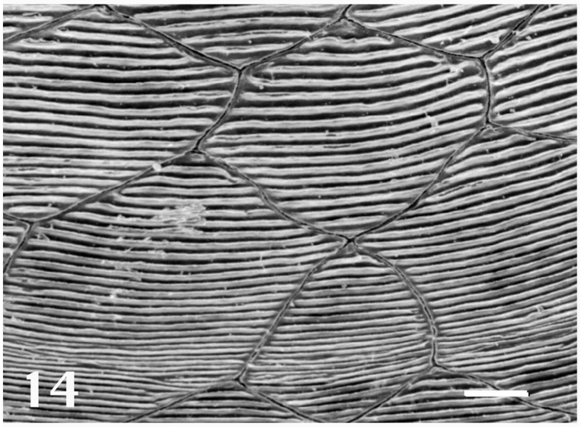
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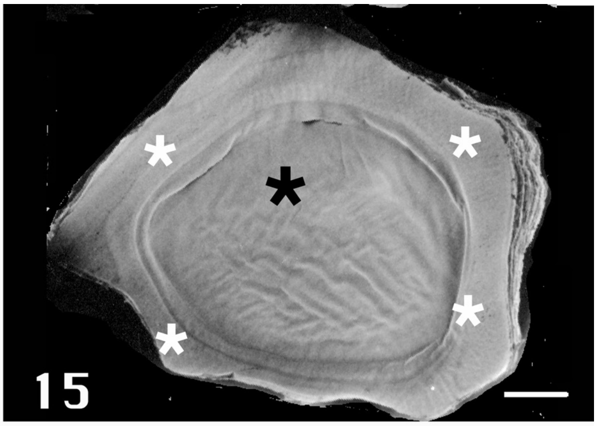
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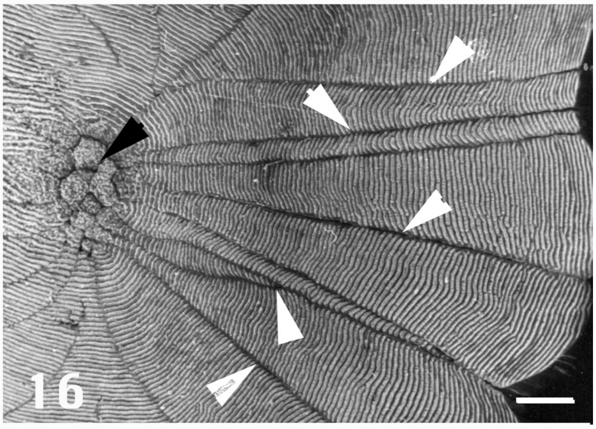
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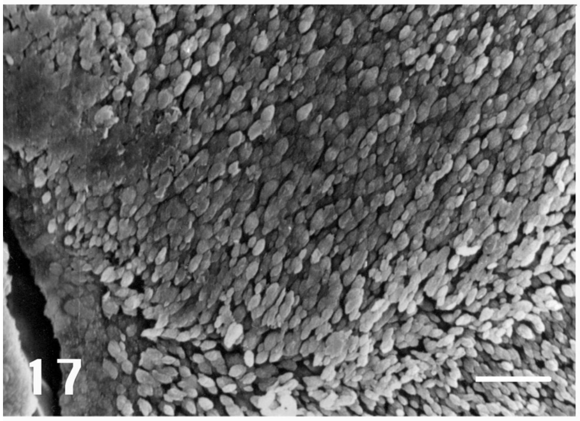
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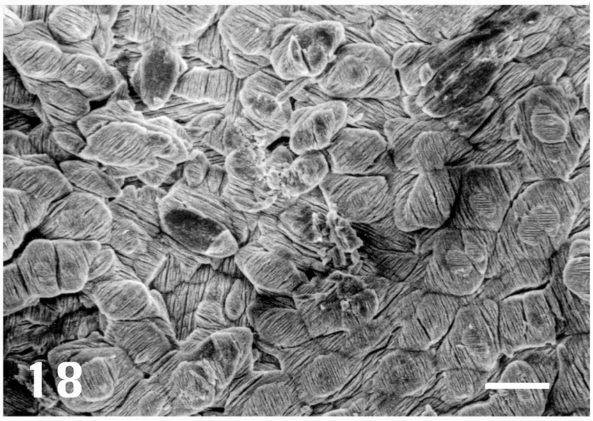
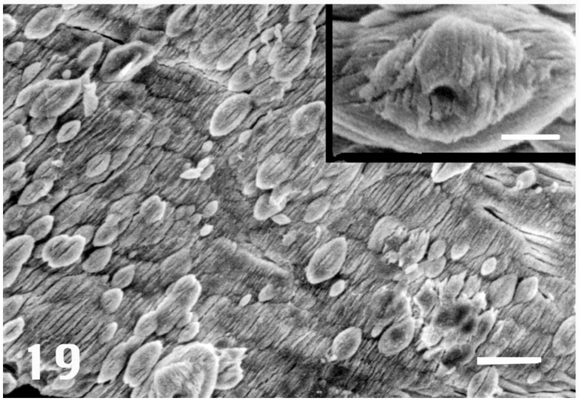
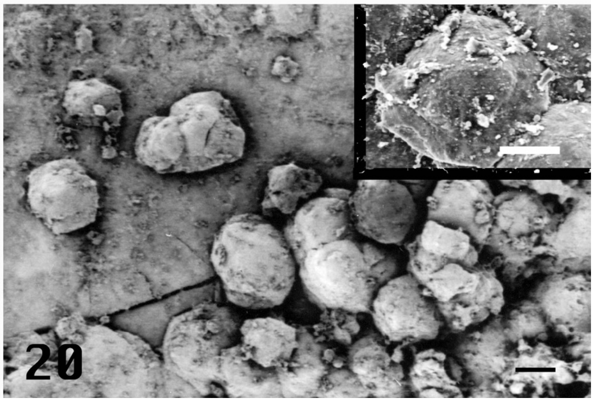

18


19


20

terids, ganoin has been shown to be epidermal in origin (Ørvig, 1977; Sire *et al.*, 1986, 1987; Meunier *et al.*, 1987; Sire, 1994, 1995; Zylberberg *et al.*, 1997). The ability to produce ganoin has been reduced during evolution and has entirely disappeared in the taxa that possess elasmoid scales such as Amiidae (Kerr, 1952; Meunier, 1980; Meunier and Poplin, 1995), †*Pachycormus macropterus* (this study) and extant basal Teleostei (this study).

Another evolutionary feature of ganoin scales is the progressive reduction of the superficial odontodes (*sensu* Ørvig, 1977; Richter and Smith, 1995). They are attached to the scale surface in Lepisosteidae (Nickerson, 1893; Gayet and Meunier, 1993), and they also occur in †aspidorhynchids (Brito and Meunier, 2000). The odontodes have not been found in the other species with lepidosteoid type of scales studied here. Odontodes are absent in the scales of extant teleosts (Sire, 2001). However, dermal denticles are present on the anteriormost scale of the median row in the clupeomorph *Denticeps clupeoides* (Sire *et al.*, 1998), on the dermal bones of the head of the atheriniform *Atherion elymus* (Sire and Allizard, 2001) and on the dermal plates of certain armoured catfishes, including Callichthyidae and Loricaridae (Bhatti, 1938; Sire and Meunier, 1993; Sire and Huysseune, 1996). In these catfishes, the authors usually interpreted these plates and their dermal denticles as homoplastic elements compared to those found in basal actinopterygians (Fink and Fink, 1981).

In the lepidosteoid type of rhombic scales, the bony basal plate is deposited first (Nickerson, 1893). The region that houses the terminal ramifications of the canals of Williamson corresponds to the initium of the scale, *i.e.* the region which is deposited first during ontogeny. This area is constituted of woven bone with embedded isodiametric osteocytes, and is frequently separated from the upper ganoin layer by several layers of either pseudo-lamellar or lamellar bone. The presence of several layers of lamellar bone between the bony initium and the ganoin layer indicates that a certain time has run between the formation of the initium of the scale and the deposit of the first layer of ganoin. The rest of the basal plate is composed of lamellar bone, forming a regular orthogonal plywood, with penetrating Sharpey's fibers. This lamellar bone is mineralized over its entire thickness. This contrasts with the elasmoid scales of the species studied so far (Meunier, 1984b, 1997; Zylberberg *et al.*, 1992), in which the basal plate is uncompletely mineralized (cf. isopedin *sensu* Meunier, 1987, or elasmodin *sensu* Schultze, 1996), except in the sciaenid *Micropogonias altipinnis* (Meunier *et al.*, 2004).

The reticulated scales lacking Mandl's corpuscles in many osteoglossomorphs suggest they constitute a monophyletic group (Osteoglossidae, Mormyridae). However, taxa such as Notopteridae have typically ornamented elasmoid scales devoid of squamulae, and possessing Mandl's corpuscles. This could mean that recent Osteoglossomorpha include at least two lineages. The presence of Mandl's corpuscles in the scales of †*Laelichthys*, an extinct teleost closely related to Osteoglossidae, raises, therefore, a phylogenetic problem because such corpuscles are a general feature of elasmoid scale mineralization as described in extant dipnoans (Zylberberg *et al.*, 1992), and in *Latimeria* (Meunier and Zylberberg, 1999). Mandl's corpuscles can be therefore considered plesiomorphic for elasmoid scales and the squamulae with a "box-like" mineralization (Meunier, 1984a, 1984b) are apomorphic features for scales of extant Osteoglossidae. As revealed by its scales †*Laelichthys* must be considered either a potential ancestor of the osteoglossids or being located outside the osteoglossid clade.

Transformation from ganoid scales to elasmoid scales

The upper region of the scales of †*Pholidophorus*? sp. from the Late Jurassic of Normandy (France) presents two layers. A deeper, typical, pluristratified ganoin layer, the lamellae of which are about 10 µm thick and an upper layer that enters in contact with the bony basal plate at the scale margins and that partly overlies the ganoin layer. This outer layer is constituted by thin irregular lamellae of a hypermineralized substance (Figs 3, 4), but its surface is not ornamented with the tubercles that are typical of the ganoin. In fact, there are no reasons to identify this outer layer as ganoin. This layer might be either degenerated ganoin or a

Figures 13 to 20. - Scanning electron microscope observations. • Figure 13. - *Marcusenius ussheri*. Overview of the scale surface showing reticulated grooves delimitating squamulae in the anterior (AF) and posterior field (PF). Scale bar = 0.5 mm. • Figure 14. - *Marcusenius ussheri*. Detail of the anterior region showing several squamulae; the superficial ornamentations consist of circuli. Scale bar = 50 µm. • Figure 15. - *Marcusenius ussheri*. Detail of the mineralizing front of a squamula; the center (black asterisk) of the squamula is concave and its margins are thicker (white asterisks). Scale bar = 50 µm. • Figure 16. - *Hoplias aimara*. General view of the focus (black arrowhead) and the anterior region (on the right) showing several radii (white arrowheads) and circuli. Scale bar = 1 mm. • Figure 17. - *Notopterus notopterus*. General view of the mineralization front at the deep surface of the scale showing numerous ovoid Mandl's corpuscles. Scale bar = 100 µm. • Figure 18. - *Megalops atlanticus*. General view of the mineralization front showing numerous more or less rhomboidal Mandl's corpuscles. Scalebar = 50 µm. • Figure 19. - *Clupea harengus*. General view of the mineralizationfront showing numerous ovoid Mandl's corpuscles. Scale bar = 25 µm. Inset: detail of a quadrangular Mandl's corpuscle. Scale bar = 10 µm. • Figure 20. - †*Laelichthys ancestralis*. General view of the deepest face showing typical geometrical reliefs that are true Mandl's corpuscles; the mineralization front has been conserved during fossilization. Scale bar = 50 µm. Inset: detail of a rhomboidal Mandl's corpuscle. Scale bar = 25 µm.

neoformation, the origin of which is unknown (either dermal, epidermal or both?). It resembles the outer-limiting layer of the teleost elasmoid scales. Additional palaeohistological examination of fossil taxa possessing both ganoid and elasmoid scales in their squamation are needed to better understand the nature of this peculiar upper layer.

The superficial region of the teleost elasmoid scales is made of two layers (Schönbörner *et al.*, 1979; Zylberberg and Meunier, 1981; Zylberberg and Nicolas, 1982; Sire, 1985; Sire *et al.*, 1997b; Sire and Arnulf, 2000). The first-deposited one (the external layer), located above the basal plate, has a bony-like structure, that contains bone cells (in primitive taxa) or not (in derived taxa). The external layer is frequently covered by an outer limiting layer deprived of collagen fibrils, and often only located in the region covered by the epidermis. This outer limiting layer thickens during ontogeny and, in that case, it shows fine incremental growth lines (Fig. 12; see also Sire, 1985; Meunier, 1997). In some taxa, e.g. *Osteoglossum biccirhosum*, the limiting layer matrix merges with the external layer matrix, but patches of its matrix are always clearly visible (Meunier, unpubl. obs.). According to the data available, we interpret the outer limiting layer as a neoformation in teleost elasmoid scales; but in which taxon did it first appear? The formation of this outer limiting layer is probably controlled by epidermal-dermal interactions (Sire *et al.*, 1997a, 1997b).

To understand the transition "lepidosteoid scale-elasmoid scale", account must be taken of an important evolutionary constraint: the improvement of swimming ability requiring the substantial lightening of the skeleton, especially squamation, without a concomitant reduction of its hydrodynamic properties (elasticity, strength, and stiffness), that maintain energetic economy (Burdak, 1979). All these factors have involved the following morpho-anatomical novelties: disappearance of odontodes, reduction of the ganoin layer and reduction of mineralization. The elasmoid scales become imbricated, which allows conservation of the function of protection; the diameter of collagen fibers thickens significantly, as does the thickness of the collagen layers in the basal plate, and the collagen fibers are organized into a complex 'plywood-like' network (Meunier and Castanet, 1982; Meunier, 1987-88). All these characteristics of the collagen matrix improve strength, stiffness (even when mineralization is lacking), elasticity, and hydrodynamic properties (Burdak, 1979). This phenomenon is also observed in various taxa belonging to the Sarcopterygii and Actinopterygii (Schultze, 1977; Meunier, 1984b). The external layer being the first deposited matrix in elasmoid scales (Yamada, 1971; Lanzing and Wright, 1976; Sire and Géraudie, 1983; Sire *et al.*, 1997b), it is considered homologous to a "bony initium". The basal plate shows a more or less complex spatial organization (double-twisted plywood: Meunier and Castanet, 1982) different from that observed in lamellar bone, an orthogonal collagen network. Yet, in the scales of the various fossil taxa examined in the present work, the basal plate, deposited after the bony initium (in which we can see the ramifications of the extremities of canals of Williamson), is a typical orthogonal 'plywood', in which the lamellar bone structure is constituted of thin lamellae (0.5-2 μm thick) with collagen fibers 20-50 nm diameter in average. We consider this lamellar bone homologous to the isopedin organization (*sensu* Meunier, 1987; = elasmodin of Schultze, 1996) of an elasmoid basal plate.

Conclusions

The present study of the morphological and histological structure in basal teleost scales has shown that:

1- there is a reduction of the ganoin layer until its complete disappearance. There is also a reduction of mineralization in the basal plate;

2- there is a process of acellularisation in elasmoid scales, first in the "basal plate" (elasmocytes), followed by a loss of cells (osteocytes) in the superficial layer;

3- the "basal plate" in teleosts is homologous to the bony basal plate of the ganoid scales. Moreover, the double-twisted 'plywood' of the scales of extant basal teleosts appears to be an apomorphy, compared to the orthogonal 'plywood' found in the †aspidorhynchids and "†pholidophorids";

4- two types of mineralization are found in the elasmoid scales: one with Mandl's corpuscles (e.g., scales of all taxa except in mormyrids and osteoglossids), and one with a "box-like" mineralization in mormyrids and osteoglossids, except in *Arapaima*;

5- in the evolution of the "basal plate" in teleost scales, the bony tissue composed of thin collagen fibers (less than 50 μm in diameter) changes into a derived tissue with thick collagen fibers (50 to 150 μm).

In addition to these observations, the following conclusions concerning basal teleost phylogeny can be drawn:

1- the clade "Teleostei" comprises taxa possessing scales of the lepidosteoid type and other taxa showing scales of elasmoid type;

2- despite controversies concerning the phylogenetic position of the aspidorhynchids, scale morphology and histology in this group do not differ from that of other "basal teleosts" such as †*Pholidophorus bechei*. However, among the taxa examined, aspidorhynchids are the unique group that possesses odontodes on their scale surface, a character which is considered a plesiomorphy;

3- the presence of radial superficial structures above the bony basal plate (amioid-type scales) in †*Pachychormus* indicates that this taxon is not a teleost;

4- elasmoid scales are a unique character of teleosts above the level of †*Pholidophorus bechei*;

5- some osteoglossids possess a different type of scale, with squamulae on the overlapped field. This type of scale is proposed to be called osteoglossid-type of scale. They are considered derived features within the osteoglossid clade.

Acknowledgements. - The authors thank Hans-Peter Schultze for manuscript improvements and for helpfull scientific discussions about the scale structure in primitive actinopterygians and basal teleosts. The critical reviews by G. Arratia, M. Richter, and M. Laurin have improved the manuscript. Dave M. Martill improved style and grammar of the English manuscript. PMB's research was supported by the CNPq and by an Invited Researcher Grant from the Muséum national d'Histoire naturelle of Paris. The SEM data were obtained with the technical support of Christiane Chancogne (Laboratoire de Paléontologie, MNHN Paris).

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Reçu le 06 novembre 2003.
Accepté pour publication le 25 mars 2004.